Dear Editor,
Thanks for the opportunity to provide a revised version of our manuscript addressing reviewers' comments. We received input from four different reviewers, who all found the manuscript interesting and with important contributions, but mostly limited by our lack of detail in the presentation of some aspects of the study.

Here, we provide a one-to-one answer to all reviewer comments and a new version of the manuscript with improved descriptions of several aspects of our research. The main changes introduced in this new version are: 1) we added additional details about the incubation setup, the modeling analysis, and the interpretation of the results. 2) A new table presenting the results from the main optimization. 3) A modified version of Figure 4 that gives less emphasis on the obtained dependence and sensitivity curves, but more on the predictions for the specific experimental treatments. 4) We added a new figure (Fig 5) showing the interacting response of the decomposition modifier ξ to the different treatment combinations. This new figure helped us to better explain our results. 6) We added 'in a boreal forest soil' to the title to better define the scope of our study.

We hope this new version addresses well all previous comments and it is now suitable for publication.

Reviewer 1

We thank reviewer 1 for his comments and for actively engaging in the discussion motived by this manuscript (see comments to Reviewer 4). Here we quote his comments in *italics* and provide our answers below each major comment.

This paper reports a relatively simple factorial experiment of soil respiration response of moisture, temperature and oxygen. This is an important topic if we are to accurately model respiration of soils in temporally and spatially variable environments. One might think that these relationships have been well constrained already but when trying to find specific examples in the literature it is not easy to find many examples. A simplification of the DAMM model is used to explore data. A nice addition is inclusion of an oxygen treatment to distinguish between the role of water in controlling oxygen supply and carbon diffusion. The paper is easy to read and follow and I generally have few comments. I am not really expert in modelling side of soil carbon dynamics and will limit my comments here.

We think one of the reasons there's relatively little work on this subject is because the difficulties in controlling three factors simultaneously. Full factorial experiments involving more than two factors are not so common in ecology even though they can help us to better understand multiple factor interactions among environmental drivers.

Specific comments 1. While a high C content soil was supposedly selected to avoid carbon limitation during the incubation this does not mean that the labile fraction of C would not be depleted. This is important as it is possible for depletion of labile C occurs faster at higher temperatures. The authors can check

whether this might have occurred by examining the timeline of CO2 production if carbon supply was not limiting then respiration rates should be linear and not reach a plateau. Do authors have this information? Currently reporting only the total CO2 after 35 days.

We do have this information. Cumulative CO_2 production from all treatments is presented in the Figure 1 below.

The treatments with the highest amounts of respired CO_2 showed almost linear increases in respiration and provide no evidence of a depletion of labile carbon. Treatments with low water filled pore space (WFPS) and low oxygen levels show a tendency to reach a plateau, but this is likely due to a strong decrease of respiration rates due to water and oxygen limitation and not due to substrate depletion. The soil is the same for all treatments so we expect labile carbon to be the same in all cases.

The results from the model optimization shows that the fraction of fast 'labile' carbon is around 56% of the total initial carbon in the incubations (Table 1 in new version). This is common for these highly organic soils and it is highly unlikely that this labile carbon is depleted during a 35-day incubation.

2. Alternatively, a rise in rate through time would indicate adaptation and/or microbial growth during the incubation. Are the authors confident during the 35 days that microbial adaption to constant moisture, temperature and oxygen conditions has not occurred? If this does occur then the model fitting data between different microbial populations. The authors need to acknowledge these possibilities and present some information or rationalisation to overcome them.

The cumulative respiration data in Figure 1 presents clear and distinct trends for each of the treatments. Treatments with high levels of temperature, moisture and oxygen show near linear trends, which is an indication that the microbial communities are growing at an almost constant rate and are not experiencing any resource limitation. In treatments with low resource levels (moisture and oxygen), microbial growth declines during incubation time suggesting depletion of resources necessary for growth. We do not believe that the linear trend in high-resource treatments is an indication of microbial adaptation that somehow would invalidate our results. On the contrary, this is a strong indication that growth, and therefore respiration rates, is not limited by the levels of available resources. More importantly, the slope of the near-linear increases in these treatments is highly dependent on the factor levels, a strong indication that rates depend on the three main factors imposed, something that is later backed up by our modeling analysis.

3. What was the temperature range in the field that the soils are exposed to? This soil was collected from the active layer at a Caribou/Poker Creek watershed in central Alaska. The active surface layer is exposed to large changes in temperature during the year, from a minimum temperature close to -19°C to a maximum of 18°C, so the annual temperature range is close to 40°C. This information was obtained from the Bonanza Creek LTER site, data summaries for the CPCRW station (`http://bnznet.iab.uaf.edu/vdv/vdv_historical.php`). We included this information in the site description section of our manuscript.

4. What bulk density was the soil packed to in the cores? Do these represent

what might be observed in the field?
Each cylinder had a volume of 1570 cm^3 (10 cm diameter, 20 cm height), and contained 450 g of soil. About half of the cylinder was filled with soil, so the approximate bulk density was 0.57 g cm^{-3}. Typical values for bulk density in organic horizons and peats are between 0.1 and 0.5 g cm^{-3} (Hossain et al., 2015). We believe the bulk density within our cylinders was realistic and corresponds to typical values for these type of soils.

5. Pg 3 8 is fallowed meant to be followed?
Changed.

6. Pg 4 ln 5-10 Include abbreviations O, Ko, W in text
Done.

7. Pg 4 ln 23 There were only two temperatures used so that statement respiration did not decrease at higher temperatures should strictly be singular "at the higher temperature".
Changed as suggested.

8. What are the error bars on fig 2? Fig2 I also printed this out in black and white and it was very difficult to see what line was what, symbol could be changed and a dashed line used.
Arrows represent 25 and 75% quantiles of the distribution of the parameters obtained through Bayesian optimization. This information was added to the figure caption. Symbols in figure were changed to improve readability in white-and-black print outs.

9. Figure 2 and 3 this not really my area and I think a little more description of what these graphs mean would be useful.
We added more description on the main text and on the figure captions.

10. Figure 4 is it reasonable to make prediction of a full curve of temperature response based two temperatures? And furthermore make prediction above and below the temperature measured? Similarly a very steep curve is predicted for the oxygen content response between two end points.
Good point. Here we only wanted to show the predictions from a model that fitted well the data at the specific points within possible ranges for the controlled variables. We believe it is also interesting to know what the model predicts within and outside the range of possible values. However, one must be very careful with the interpretation of these results since, as the reviewer points out, we do not have data outside the specific points where we imposed our treatments.

To address this issue we modified Figure 4, showing explicitly predictions for the specific treatment combinations where we have data, and only plotting the predicted curves as dashed lines for reference.

11. Pg 7 ln 5. I disagree with the statement of increases in temperature being almost always associated with decreases in soil moisture is really a matter of temporal scale of interest. For example between seasons this is certainly possible wet and cold vs hot and dry and this would allow microbes time to adapt. But increases in temperature diurnally can also occur. It would be not unusual for a soil to cycle by 5 to 10 C during a 24 hour period where moisture content would be steady and there is less time for adaptation.
Yes, this is a matter of scale. At some time scales, increases in temperature are

accompanied with increases in moisture (e.g. as soil unfreezes), it may dry at other scales (e.g. in the spring season in mediterranean ecosystems), or it may remain constant during a 24 hour cycle. We explored these different dynamics in a previous manuscript (Sierra et al., 2015b, Fig 1), and concluded that in a large number of relevant cases, soil temperature and soil moisture change simultaneously.

12. Pg 9 Conclusions and discussion. That the authors did not find a decline in respiration at a single higher temperature (35C) but this does not mean that MMRT or similar functions are not important in moderating microbial responses in soil. The authors only had two temperatures 25 and 35 C. For the respiration rate to be lower at 35C than 25 C would require the temperature optimum (temperature at which the respiration rate is maximal) to be closer to 25C than 35C. If a temperature optimum for soil respiration was near or greater than 35 C there would be no observed decline in respiration in comparison to the rate at 25C. If I have my logic correct then there is no support for the argument in the conclusions that scale in this case matter with respect to extrapolating MMRT from enzymes to soil systems.

The reviewer is right here, and we acknowledge that our logic was flawed. It is correct that our two temperature treatments may not be enough to observe any potential decline in respiration rates as predicted by the MMRT, and this has little to do with scales. However, we still believe that there's an important mismatch between the scale at which the MMRT operates and the scale for observing soil respiration in soil cores and soil pits. The MMRT predicts a decline in respiration at high temperature provided all other environmental factors remain constant. But in most cases in soils, both temperature, moisture and oxygen change simultaneously. Our point with the manuscript is to bring to the attention that these interactions are very important for predictions at the soil core level, even though there may be mismatches with the predictions at the enzyme level.

To address this comment we re-wrote the conclusion section and are now more precise about the limitations of our experiment and the mismatch among scales.

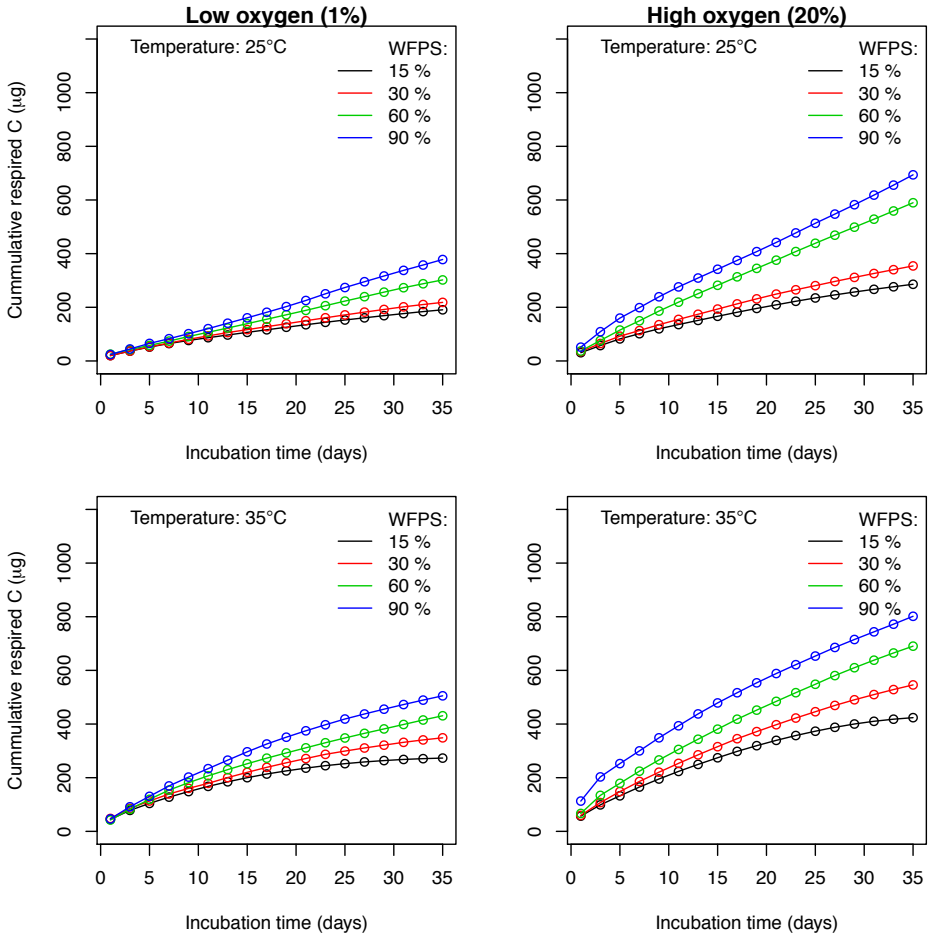

Figure 1: Cumulative respiration for all treatments in the incubation experiment.

Reviewer 2

We thank reviewer 2 for his/her comments on our manuscript. Here we quote comments in *italics* and provide our answers below each major comment.

p. 3, line 5: The soil columns contained 450 g of homogenized soil. It would also be good to have an idea of the dimensions of the columns (diameter, height). This determines, for instance, the surface area that is subjected to drying and the distance that the oxygen flow travels through the sample. Further, an estimate of the bulk density of the soil or of the proportion of pore space in the samples would be helpful. It is especially important that the pore space was similar for all soil columns so that differences in diffusion potential of oxygen, water and temperature does not influence the results.

For each cylinder, we had 450 g of soil in a volume of about 785 cm^3, which results in a bulk density of about 0.57 g cm^{-3}. This was similar for all samples and care was taken to have similar bulk density across all treatments.

It is important to keep in mind that soil water modifies the amount of filled pore space, and for this reason our moisture treatment is expressed in water-filled pore space. This obviously has consequences on the diffusion characteristics for each moisture treatment, which results in the observed differences in respiration rates.

p. 3, lines 9-11: One of the reason to choose Arctic soils that is mentioned is the low temperatures at which its microbial community is constantly exposed, which facilitates the possibility of observing strong responses at the extreme of the temperature range. I agree that one would expect a strong response of the microbial activity after step-increasing the temperature by ∼20 to °40C, but the reaction might be more related to stress physiology than an actual temperature response, especially during such a short treatment period (35 days). Therefore, I would not stress this point too much and briefly touch the issue with stress responses after drastic step-change in environmental factors in the discussion section. Additionally, I suggest to add another advantage of using Arctic soils for this incubation study: The large amounts of C stored in the Arctic region in combination with the fast warming (compared to the global average). Also moisture (and oxygen) is an issue in that region because of the impenetrable permafrost layer that is present under a large part of the surface. Further, it is important to restrain your conclusions to Arctic soils, as their dynamics might differ from soils from more moderate or tropical climates. For instance, it has recently been shown that the C balance of soils from Arctic and subarctic regions are more sensitive to warming. It might be that the influence of moisture and or oxygen (and especially the interactions) differ between climates (and probably soil types, but it would dilute the story too much to dig deeper into this). It would be very interesting to perform a similar study with soils from different climate regions.

These are all good points. The reviewer is correct in that the high temperature treatments we applied may induce physiological stress in microbes. The effect may be expressed as a short-term physiological response or as a long-term change in microbial communities (Schimel et al., 2007). Our CO_2 respiration

measurements however, cannot distinguish between these two type of responses. Although our incubations were short (35 days), this is still enough time for the microbial community to shift. We may not be able to say anything here about the mechanistic response at the microbial level, but we observed an aggregate response that may combine both microbial physiology and community composition. At the level of abstraction we are focusing in this manuscript, this overall response is important for representing climate change effects in soil models.

We also agree with the reviewer in that it would be very interesting to replicate this experiment for soils from different ecosystems. We may be able to observe very different responses for tropical or temperate systems.

We added some text to the methods and discussion section addressing these points.

p. 4, line 4-6 and 24-25: The fractionation of slow and fast cycling C pools (with different decomposition rates) is not well introduced. Add a paragraph in the introduction as rationale why it is interesting to separate into slow and fast cycling pools when investigating temperature, moisture and oxygen effects on decomposition rates. Also, expand the discussion on this subject.
This is an important point that we did not address properly in our previous version. It is not only the interaction among multiple environmental factors, but also how they affect different rates. Our modeling approach includes both a fast and a slow pool that are modified by these different environmental factors. We included some text in the introduction, the model description, and the discussion addressing this topic.

p. 4, line 4-6: Define T, W and O. I would also change W (Water) into M (Moisture), which fits better with the title.
Definitions were added, and W was changed for M as suggested.

p. 4, line 21 and 22: 35, 90, 20 and 25, 15, 1: Add units to the numbers.
Done

p. 6, line 3-4: Decomposition rates were highly sensitive at a narrow part of the oxygen range, while for moisture this range was wider (Figure 4). The oxygen range in this study covered the full range of oxygen that can be expected, from 1% (anoxic) to 20% (the maximum that can be expected; atmospheric O2 con- centration). The range with the highest sensitivity to oxygen in Figure 4 runs from 0 to 2.5%, which is about 12.5% of the range. Also for moisture a broad range is covered (15 to 90%). The range with the highest sensitivity to oxygen in Figure 4 runs from 0 to 10%, which is about 11% of the range (if the maximum is set to 90%). As there is little difference between 12.5 and 11% of the range, I do not understand the statement that the sensitivity to moisture occurred at a broader range. Can you explain this in more detail?
Our previous description of the intrinsic sensitivities was ambiguous as noted by the reviewer. We re-wrote completely this paragraph in light of other reviewer's comments and the modification of Figure 4. We do not refer here about these ranges anymore, but mostly to the overall shapes of the dependence and sensitivity curves. We also put more emphasis on the predictions for the specific treatment levels and not so much on specific predictions outside the values for which we have no data.

p. 8, Figure 4: It is strange that the strongest response for all three parameters occurs outside the treatment range of this study. Is it possible to extrapolate your findings that far?
Figure 4 was modified to avoid emphasis on interpretations outside the ranges where we do not have data. The new version of Fig 4 gives more emphasis on the specific treatment levels where we have measurements, and we only provide model predictions outside these values as a reference for the functional response of the model.

p. 1 line 7; p. 3 Lines 9; p. 9 line 8 Change "arctic" into "Arctic"
As Reviewer 3 pointed out, the site is really a boreal and not an Arctic ecosystem. We changed arctic to boreal throughout the manuscript.

Reviewer 3

We thank reviewer 3 for his/her comments on our manuscript. Here we quote comments in *italics* and provide our answers below each major comment.

P1 Line 7: The site is boreal, not arctic.
Yes, we changed to boreal.

P1 Line 9: The conclusion about temperature effect need to be tempered or qualified in the context of the limited range of temperatures evaluated.
We modified this sentence slightly, not mentioning that decomposition 'increases' with 'increases' in temperature, since we only have two temperatures; but mentioning that decomposition rates 'were high' at high temperatures provided oxygen and moisture were not limiting.

P1 Line 10: This is a significant conclusion, even though it seems relatively obvious- having a good experimental design to say this conclusively is useful.
Thanks.

P2 Line 4: How does this 45C threshold correspond to your high temperature? Is 45C broadly constant across ecosystems?
We mention this 45°C threshold only to introduce the MMRT, which is supposed to operate at lower temperatures than this threshold for enzyme denaturation.

P2 Line 24: True, and a major strength of this study.
Thanks.

P3 Line 8: Again, boreal, not arctic.
Changed.

P3 Line 9: This statement is not necessarily true depending on the content of labile, readily respired substrate. It should be explored a little further and contextualized with other studies that evaluate substrate limitation of soil respiration in organic soils, especially from boreal regions.
We believe that high organic soils minimize the potential of substrate limitation, but the reviewer is right in that this may not be the case always. For clarity, we added the word 'may' to this sentence.

P3 Line 18: It is unclear exactly how this measurement was used to evaluate the soil respiration or decomposition rate. Can you please clarify? Was it evaluated as change over a set time interval, or as increase over the known background from the input air? At what frequency was this measured?
For each cylinder, fluxes were measured every other day as the difference in concentration between the output and input air, multiplied by the air mass flow rate. We added a more detailed description about the quantification of respiration rate to the new version of the manuscript.

Eqn 1: Please be clear about what exactly dC/dt represents. Is it the instantaneous or the cumulative dCO2, is it CO2 or CO2-C?
Here, dC/dt represents the instantaneous change in the carbon content for the incubated soil. The respired CO_2-C is obtained after solving the system of differential equations and calculating the output flux from the numerical output. We added more details on the model description to make this clear.

P4 Line 10: Does this mean that gamma also varies by each treatment level? And initial C1 and C2 also vary by treatment level? I would like to see some

presentation of the actual C fluxes, and the change in C1 and C2 over time.
Yes, the values of γ change for each treatment level for the first optimization and this is presented in Figure 2. For the second optimization, we obtain a probability distribution for γ, which is presented in Figure 3.

P4 Line 12: Fitting the full model in eqn 2, is gamma now fixed? Also, are there limitations to fitting a q10 function with only two temperature points?
Again, for the second optimization, where equation 2 is set explicitly, we obtain a probability distribution for γ. It is not a value that changes from one treatment to another, but a range of values with some probability.

The main limitation of fitting a Q_{10} function with two temperature values is that the obtained uncertainty range is very high, which is evident in the probability distribution presented in Figure 3, and the predictions in Figure 4.

P4 Line 14: Thanks for presenting this supplement.
Thanks for the comment.

P 4 Line 27: I am more surprised at how similar the k1 and k2 values in Fig 2 are across such a broad range of O2: Can you explain this result more clearly.
This is well explained by the sensitivity functions in Figure 4. The intrinsic sensitivity of decomposition rates with respect to temperature is higher for temperature, intermediate for moisture, and lower for oxygen for the treatment levels we selected.

P5 Line 5: Can you please elaborate a little further on fig 3? We do see a few seemingly high correlations that might be worth describing in more detail. For instance, Ko and ks.
Here the concept of 'high' correlations is relevant. For exploring collinearity between parameter sets we are interested in finding correlations above 90-95%. This would be indicative that parameter values lie within a straight line. In analyses of ecological data, researchers often describe correlations above 0.3-0.4 as 'high' due to the inherent variability of ecological processes. However, the aim here with Fig 3 is to find near linear correlations as evidence of collinearity among parameter values. Therefore, we do not consider the obtained correlations as high for the purpose of our analysis.

P5 Line 6: Am I missing the posterior parameter estimates? It would be very useful to have a table of these parameter values and credible intervals.
We added a table with these parameter values and their uncertainty.

P5 Line 7: Why did you use this range rather than the 2.5-97.5? It looks like your estimates of the temperature function might be challenging in that case, which isnt that surprising with only two temps. I think it is worth revising these figures to have both the 25-75 and then standard 95% credible interval presented.
We included now the 5 and 95% interquartile ranges for the second optimization.

P7 Line 1: The discussion should give some analysis of the temperature response. In particular, how do the estimated q10 values compare to other q10 values using soils from similar boreal forest sites? Also, what is the temperature range at this site? You describe the 45C threshold in the introduction, but then use a much lower temperature as the high temp. Is this higher than temperatures the soil organisms at this site regularly experience? Is it higher than projected future temperatures for this site?

Our new version of the manuscript includes a discussion on the obtained dependence and sensitivity functions for temperature, moisture, and oxygen, but we do not include a discussion on comparing the obtained Q_{10} values with others found in the literature.

The objective of our modeling analysis was to obtain relevant parameters for the interpretation of the experimental results. We are not concerned here on describing or interpreting our parameter values as representative for modeling this type of soils under non-experimental conditions. Under field-conditions other physical and biological processes may have also a strong effect on decomposition and respiration rates not relevant under the experimental conditions of our experiment. For this reason, we are reluctant to compare the dependence function and the Q_{10} values against others found for other type of soils under completely different measurement, experimental, and modeling setups. Previously, I have strongly criticized the practice of comparing Q_{10} values from different studies using different functions (Sierra, 2012), and do not consider appropriate to do such a comparison here.

P8 Line 3: Can you please describe some of these interactions more specifically? It seems as though a lot of the work is presenting marginal responses. Is there some reduction of temperature sensitivity at high water content? or a reduction of oxygen sensitivity at low water content? Please clarify what interactions you mean.

To address these interactions more explicitly we introduce a new figure (Fig 5) calculating the value of ξ for the specific treatment combinations. This figure help us to discuss the interactions among the three variables in more detail.

P8 Line7: I am not sure I follow. Looking at figure 1, most CO2 was respired at high water content. Are you thus comparing the low to the high oxygen rates, and then inferring a response in the absence of continuous oxygen flow? Please be explicit about that.

This sentence refers to the study of Tucker and Reed (2016) and not to the results presented in our manuscript.

P9 Line 3: Perhaps discuss more thoroughly how the inclusion of dynamically changing air-filled pore space might relate to your results. This is a suggestion, not a necessary revision.

We extended this paragraph to give better details about how the model can be modified for representing more complex processes or for applications to the field level.

Technical corrections

*P1 Line 16: *significantly*

Done

1 Reviewer 4

We thank reviewer 4 for his/her comments on our manuscript. Here we quote comments in *italics* and provide our answers below each major comment.

First, there is some confusion in describing the level off of decomposition rates at high temperatures. E.g. at P2 L6, enzyme denature should be described as irreversible enzyme denature, so one will not confuse it with reversible enzyme denature. As a mater of fact, the MMRT theory is largely based on reversible enzyme denature (though its authors did not say so), which was known as early as in the 1980s (Murphy et al., 1990: Common features of protein unfolding and dissolution of hydrophobic compounds, Sciences). The idea was then combined with the concept of a single rate-limiting master reaction to model the respiration of bacteria by Ratkowsky et al. (2005: J of Theoretical Biology). A much earlier study by Sharpe and DeMichele (1977: J. Theoretical Biology) also derived a similar curve as MMRT, and was used in the model ECOSYS (Grant et al, 1993: Soil Biol. Biochem.) to simulate microbial decomposition. More recently, the same idea was applied in the model Tang and Riley (2015: Nature Climate Change). I think the authors of this study should report these developments so readers will have a more complete picture of this problem.

It is incorrect to say that the MMRT is based on reversible enzyme denaturation. The answer to this comment by Reviewer 1 clearly explains why this is not the case, and our explanation that MMRT describes the changes in activation energy with temperature is in fact correct. Furthermore, we believe that a discussion on the origins of one enzyme-level theory over another is well beyond the scope of this manuscript. Our measurements and level of abstraction are at the level of overall respiration fluxes and how are they influenced by temperature, moisture and oxygen. We only mention the MMRT and denaturation as a context for expected responses, but a detailed description of enzyme reaction theories would introduce a level of detail that would serve more as a distraction rather than a useful context for the present analysis.

Second, P2. L10-11, I think this criticism is not quite true. Authors who applied these concepts never said moisture should remain constant; rather they just focused on temperature, because temperature is considered as the most important factor. Moisture effect could be very well incorporated into those applications, which may be under way and ECOSYS has done this in the 1990s.

This is really not a criticism, but rather an important consideration when using these functions. Temperature effects on enzyme activity and decomposition rates operate under the assumption that all else remains equal except temperature. This is very important for developing and testing these functions, but in practical applications one must also consider that other environmental factors also change. This is the only point we wanted to make here.

Third, in describing the moisture effect, the authors missed the physiological effect that the moisture will impose on microbes as soil matric pressure becomes more negative. Such effect was shown to be important in Grant and Rochette (1994: Soil Sci. Soc. Am. J.), Manzoni et al. (2016: Soil Biology and Biochemistry) and Yan et al. (2016: Biogeochemistry).

We added a sentence addressing this physiological effect.

Fourth, in describing the incubation, the geometry of the incubated soil is not clear, e.g. what is the thickness of the cylindrical soil column? Such overall thickness will definitely affect the interpretation of the empirical data.

We included a description of the area, height, and volume of the soil columns as well as a calculation of the bulk density of the soils.

Finally, in describing the modeling approach, the authors did not lay out the hypotheses that lead to their model structure. For instance, under what conditions should this model structure be assumed applicable? Apparently, the model as proposed will only be useful for a soil column neither too shallow nor too deep. For a too shallow soil in natural environment, oxygenation will be very effective under the variable environment (through mechanisms such as wind pumping), so both the oxygen and moisture effect will be hard to discern from empirical data. For a too deep soil, difference in the vertical distribution of all decomposition variables will invalidate the homogenous assumption as built in the model. Also, the model assumes the microbial dynamics is totally slaved to the moisture and oxygen effects, so hysteretic behavior due to population dynamics as identified in Tang and Riley (2015) will be missing. The population dynamics may be very important in field conditions.

The scope of application of the parameterized model does not go beyond than that of the incubated soils. It is not our objective to propose a general model that can be applied to field conditions. We were only interested in testing a model that include the three main environmental factors (Temperature, Moisture, Oxygen) on a homogeneous organic soil consisting of two kinetic pools. We acknowledge that for predicting field data a more complex model may be needed, which is expressed in the last paragraph of our discussion.

To make this point even more clear, we added a sentence in our model description section indicating that the objective of this model structure is only to explain our experimental data, but more complex models may be needed for other applications.

P3 L29-32: this could be summarized as parametric equifinality.

Yes, these are similar terms. We added the word 'equifinallity' in parenthesis so readers know that they are synonymous.

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Interactions among temperature, moisture, and oxygen concentrations in controlling decomposition rates in a boreal forest soil

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Abstract. Determining environmental controls on soil organic matter decomposition is of importance for developing models that predict the effects of environmental change on global soil carbon stocks. There is uncertainty about the environmental controls on decomposition rates at temperature and moisture extremes, particularly at high water content levels and high temperatures. It is uncertain whether observed declines of decomposition rates at high temperatures are due to declines in the heat capacity of extracellular enzymes as predicted by thermodynamic theory, or due to simultaneous declines in soil moisture. It is also uncertain whether oxygen limits decomposition rates at high water contents. Here we present results from a full factorial experiment using organic ~~arctic soils~~ soils from a boreal forest incubated at high temperatures (25 and 35 degrees C), a wide range of water-filled pore space WFPS (15, 30, 60, 90%), and contrasting oxygen concentrations (1 and 20%). We found support for the hypothesis that decomposition rates ~~increase~~ are high at high temperatures provided enough moisture and oxygen is available for decomposition. Furthermore, we found that decomposition rate is mostly limited by oxygen concentrations at high moisture levels; even at 90% WFPS, decomposition proceeded at high rates in the presence of oxygen. Our results suggest an important degree of interactions among temperature, moisture, and oxygen in determining decomposition rates at the soil-core scale.

1 Introduction

The physical environment has a strong control on soil organic matter dynamics by modulating the rates of biological activity and therefore the rates at which organic matter decomposes. Hence, environmental change produced by global warming or changes in land use, can ~~significaly~~ significantly affect organic matter decomposition rates and the capacity of soils to store carbon (Trumbore, 1997; Schlesinger and Andrews, 2000; Davidson and Janssens, 2006; Luo et al., 2016).

Among different environmental factors, temperature, moisture, and oxygen levels in soils have a strong control on the rate of soil organic matter (SOM) decomposition (Greenwood, 1961; Bunnell et al., 1977; Swift et al., 1979; Skopp et al., 1990; Davidson et al., 2012; Moyano et al., 2013). Yet, there are still large uncertainties in our understanding on how to model environmental controls on decomposition rates. For instance, many different functions have been previously proposed to represent environmental controls on decomposition rates, most functions disagree at the extremes of the temperature and

moisture ranges, and it is difficult to select appropriate functions due to large uncertainties in available data (Sierra et al., 2015b).

In particular, there is uncertainty about the shape of decomposition functions at high temperature levels. Traditional Arrhenius kinetics predict that rates of decomposition increase monotonically as temperature increases (Sierra, 2012), a behavior well supported by classical thermodynamic theory, and in particular by its second law (Reif, 2009). However, an important number of biochemical studies shows that at a certain temperature threshold, generally above 45°C, enzymes denature and lose their capacity to catalyze reactions, slowing down rates of substrate consumption (Fields, 2001). Hobbs et al. (2013) and Schipper et al. (2014) suggest that this temperature limit for enzyme denaturation may be too high to be relevant in soils, and propose an alternative thermodynamic theory that predicts a lower temperature threshold when decomposition rates reach a maximum. Their macromolecular rate theory (MMRT) is based on the idea that the activation energy in the Arrhenius equation is temperature dependent and related to negative changes in the heat capacity of enzyme-catalyzed reactions.

Both enzyme denaturalization and MMRT operate at the macromolecular enzyme-substrate level~~where single reactions occur~~, and assume that other environmental factors such as moisture remain constant as temperature increases. At larger spatial and temporal scales though, multiple reactions occur simultaneously at different rates, and different environmental factors interact with temperature. For instance, there is large empirical and theoretical evidence showing that interactions with soil moisture lead to strong changes in decomposition rates not predicted by changes in temperature alone (Bunnell et al., 1977; Davidson and Janssens, 2006; Sierra et al., 2015b; Tucker and Reed, 2016; Zhou et al., 2016).

Soil moisture plays two contrasting roles as a modulator of decomposition rates. On the one hand, soil water solubilizes substrates and increase their availability in active microbial sites through diffusion. As soil water increases, it also reduces physiological stress on microbes by reducing soil matric potential (Moyano et al., 2013; Manzoni et al., 2014) . On the other hand, as moisture increases it fills up available pore spaces and reduces oxygen levels necessary for aerobic microbial activity ~~(Skopp et al., 1990; Moyano et al., 2013; Manzoni et al., 2014)~~ (Skopp et al., 1990; Moyano et al., 2013) . Oxygen exerts an important control on the speed of aerobic decomposition for its role as an electron acceptor in the mineralization of SOM (Greenwood, 1961; Keiluweit et al., 2016). As moisture increases in soils, aeration and oxygen levels inevitably decrease.

Progress in understanding multiple-factor effects on SOM decomposition has been hindered by a paucity of experimental research (Dieleman et al., 2012; Leuzinger et al., 2011; Zhou et al., 2016). Full factorial experiments with multiple factors and levels are rare, even though they provide basic understanding on the independent and combined effects of environmental factors on decomposition. Furthermore, there has been little work studying how multiple environmental factors affect multiple decomposition rates that account for the heterogeneity of substrates and processes in soils.

Here, we use a full-factorial incubation experiment in combination with model-data integration to address the questions: i) do decomposition rates remain high at high temperatures provided moisture and oxygen are not limiting?, ii) do decomposition rates remain high at high moisture levels provided oxygen and temperature are not limiting? These questions are important because they provide insights about the best possible model structures required to represent SOM decomposition at extreme environmental conditions, and in light of global environmental change.

2 Methods

2.1 Soils and incubation experiment

We developed a full factorial incubation experiment with the manipulated treatments being temperature (25, 35 °C), soil water content (15, 30, 60 90% water-filled pore space), and oxygen concentration in the pore space (1 and 20%)~~of soil cylinders containing~~ , with soils enclosed in PVC cylinders (10 cm diameter and 20 cm height) containing in about half of their volume 450 g of homogenized soil. The approximate bulk density within each cylinder was 0.6 g cm^{-3}. Organic soil was collected from the A horizon of a boreal forest dominated by black spruce at the Caribou Poker watershed in central Alaska, USA (65° 9' 21.365" N, 147°, 29', 28.74" W). The soil is classified as a *Histic Pergelic Cryaquept* in a Gilmore silt loam series from the United States Department of Agriculture Natural Resource Conservation Service system. It has a depth of 1 m ~~fallowed~~ followed by permafrost, and a water table depth of 20 cm. Soil temperatures in the active layer fluctuate annually from a minimum of -19 to a maximum of 18°C. The carbon (C) content of a subsample of the soil used for incubations was 46.9 $\pm$ 0.1 mg C g^{-1} soil. We chose ~~an arctic~~ a boreal soil for this experiment because its high organic matter content ~~avoids~~ may avoid potential substrate limitations during incubations, and the low temperatures at which its microbial community is constantly exposed facilitates the possibility of observing strong responses at the extreme of the temperature range. In addition, soils in the boreal region are experiencing fast changes in environmental variables, so it is of high relevance to study this type of systems.

This soil is identical as the one used in a companion paper (Sierra et al., 2015a), with the exception that in that publication we used only one single treatment to illustrate results from an identifiability analysis, while here we report data from the complete full factorial experiment.

Prior to the incubations, the soil was homogenized, passed through a 2 mm sieve, and large roots ($>$ 2 mm diameter) were removed. Four replicates per treatment were placed in two climate chambers at a constant temperature each. The bottom of each column was connected to an air inlet system that continuously flushed soil columns from the bottom at a rate of 30 $\pm$ 3 ml min^{-1} with air of known oxygen ~~concentration~~ (1 or 20 %) and CO_2 (350 ppm) concentration. The headspace exiting each column (after passing through the soil) was connected to an automated multiport stream selection valve, and then analyzed for CO_2 using an infrared gas analyzer (LI-6262 LI-COR Inc., Lincoln, USA). Respiration rates, measured as CO_2 production fluxes, were calculated as the difference in CO_2 concentration between the fluxes in the outlet and inlet streams, multiplied by the air mass flow rate. Moisture loss ($\sim$1 g per day per cylinder) due to continuous flushing of dry air was compensated by adding water to replace lost of mass once every week. Additional details about the system can be found in Malghani et al. (2013).

2.2 Statistics and model optimization

Treatment means of total respired CO_2 from the 35-day incubation period (total sum for each cylinder) were compared using analysis of variance F-statistic. We used a linear ~~fixed effects~~ fixed-effects model using as independent variables the three independent treatments as well as their combination.

To evaluate the effect of the different treatments on decomposition rates, we used a simple two-pool model. In a previous analysis, we found that for incubation data no more than 3 or 4 parameters can be optimized simultaneously without encountering identifiability (equifinality) problems (Sierra et al., 2015a). When the number of parameters to identify is ~~larger~~ large and the number of observations low, the identifiability problem results in collinearity of the parameters. This means that changes in the value of one parameter can be compensated by changes in the value of another parameter without any effect in predicting the observed data. In these cases, multiple parameter sets predict equally well the data, and it is not possible to uniquely identify the best underlying mechanisms that explain the observations (Soetaert and Petzoldt, 2010; Sierra et al., 2015a). For this reason, we chose a simple model that has three main parameters and is expressed as

$$\frac{d\boldsymbol{C}}{dt} = \xi \cdot \begin{pmatrix} -k_1 & 0 \\ 0 & -k_2 \end{pmatrix} \cdot \begin{pmatrix} C_1 \\ C_2 \end{pmatrix}; \quad \boldsymbol{C_0} = C_0 \cdot \begin{pmatrix} \gamma \\ 1-\gamma \end{pmatrix}, \tag{1}$$

where the amount of C in the system (in grams) is stored in ~~pools~~ a fast and a slow pool C_1 and C_2, with corresponding decomposition rates k_1 and k_2 (in days^{-1}). The initial amount of carbon in the system C_0 is partitioned according to a proportion γ, and the environmental term ξ is a product of three functions that depend on the environment $f(T)$, ~~$f(W)$~~ $f(M)$, and $f(O)$ such that

$$\xi = f(T) \cdot f(WM) \cdot f(O) = Q_{10}^{\frac{T-10}{10}} \cdot \frac{W}{K_W + W} \frac{M}{K_M + M} \cdot \frac{O}{K_O + O}, \tag{2}$$

where K_M and K_O are half-saturation constants for the soil moisture M and soil oxygen concentration O terms. Notice that equation (2) is a simplified version of the DAMM model of Davidson et al. (2012), and it is incorporated into a model (equation 1) that tracks the temporal dynamics of a fast and a slow pool simultaneously.

The model was solved numerically using the SoilR package (Sierra et al., 2012) , and the total cumulative respiration flux was calculated from the numerical output as an integral (area under the curve) for the 35-day incubation period. We optimized two versions of the model of equation (1) to the observed data from the experiment using a Bayesian approach (Soetaert and Petzoldt, 2010). First, we optimized parameters of each treatment independently and setting $\xi = 1$. In this way we can observe possible trends in the parameters as a function of the environmental variables. Second, we pooled data from all treatments together and fitted the full model with ξ expressed as in equation (2).

All analyses were performed in R (The R Foundation for Statistical Computing, Vienna), and all code and data to reproduce our results are available as supplementary material.

3 Results

Total respired CO_2 after 35 days of incubation showed a strong treatment effect for the three main variables (F-statistic p-value < 0.001 for the main treatment effects). Interactions among all treatment levels showed statistically significant effects (F-statistic p-value $= 0.0505$) suggesting that CO_2 efflux for this soil responded to different combinations of the treatment levels

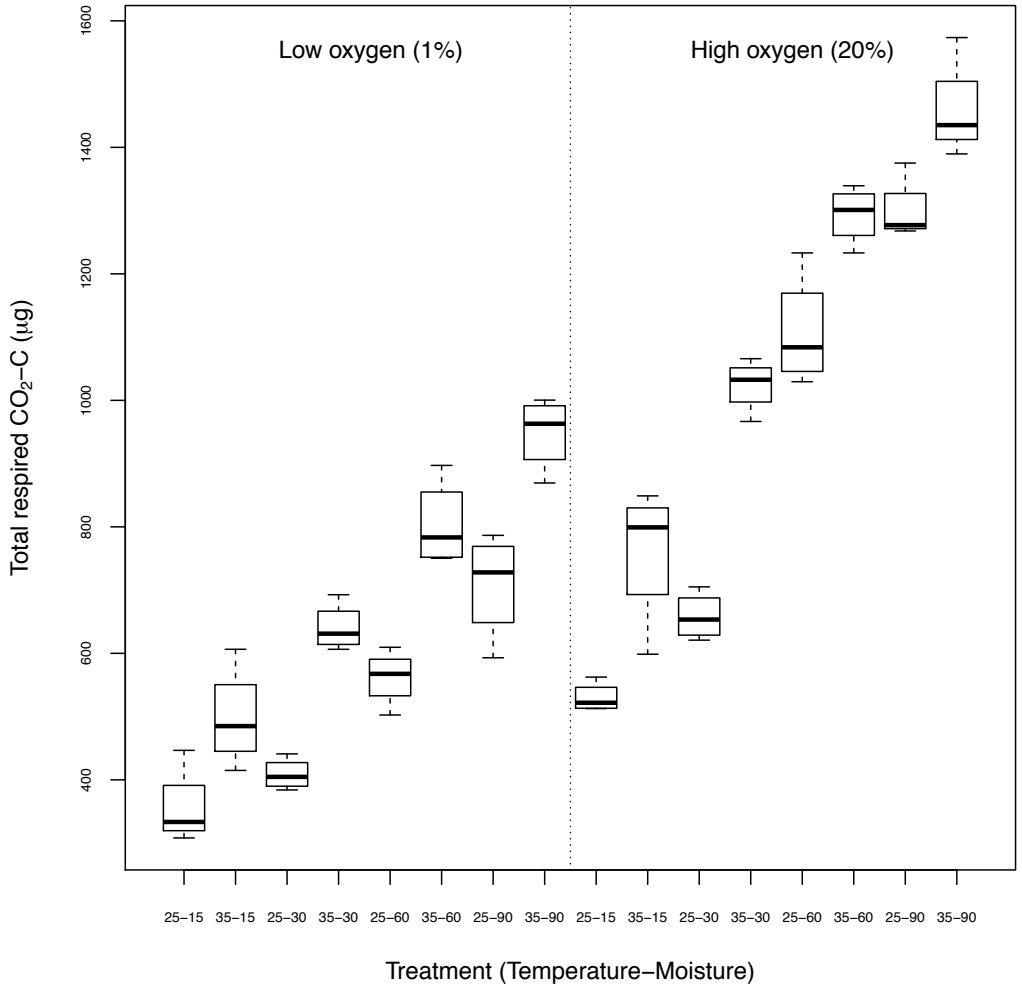

Figure 1. Total respired CO_2 integrated over the length of the experiment by treatment. Numbers in the treatment level represent the level of temperature (degrees Celsius) and soil water content (%).

(Figure 1). A statistically significant interaction (F-statistic p-value < 0.001) was also found between the soil moisture and oxygen treatments. The largest amount of respired CO_2 was observed at the treatment with the highest temperature, moisture and oxygen levels (35°C, 90%, 20%), while the lowest amount was observed at the treatment with the lowest values for these variables (25°C, 15%, 1%), confirming that these three environmental variables collectively exert a strong and significant control on CO_2 production. Total respired CO_2 during the experiment did not decrease at ~~high temperature levels~~the higher temperature level.

The results of the first model optimization showed that temperature ~~consistently~~ generally increased decomposition rates of both fast and slow pools at similar moisture and oxygen levels, but uncertainties were generally large (Figure 2). Under higher

Table 1. Summary statistics of obtained posterior parameter values for the full model of equations (1) and (2) using a Bayesian optimization procedure. Quantiles at 5 and 95% level are reported as q_5 and q_{95}, respectively.

Parameter	Units	Mean	SD	q_5	q_{95}
γ	Proportion, unitless	0.565	0.077	0.434	0.686
Q_{10}	Unitless	2.574	0.33	1.928	2.971
K_M	%	76.026	17.887	41.298	98.209
K_O	%	33.157	17.11	12.340	66.926
k_1	day^{-1}	8.25	1.411	5.455	9.891
k_2	day^{-1}	0.293	0.163	0.117	0.642

temperatures, we also observed a larger proportion of carbon being mineralized faster and contributing to the initial respiration pulse (parameter γ). At lower oxygen levels, decomposition rates were slower than in similar treatments with higher oxygen levels.

Although we estimated only three parameters, there were already ~~identifiability issues~~ problems with convergence and identifiability in this optimization (cf. Sierra et al., 2015a), which means that the obtained values of some parameters can be compensated by proportional changes in the values of other parameters. In some cases, the optimization method also failed to converge to stable posterior distributions for some specific treatment combinations. The second optimization with the full dataset reduced ~~this collinearity problem~~these collinearity and convergence problems.

The optimization of the full dataset did not provide evidence of strong collinearity as indicated by the low correlations among posterior values (Figure 3). ~~The~~ These obtained posterior values ~~indicate a strong sensitivity of ξ to temperature, and sensitivity with respect to moisture and oxygen at lower levels of these values~~ can then be summarized by simple statistics such as their mean, standard deviation (SD) and interquartile ranges (Table 1). In particular, the obtained values for γ, k_1, and k_2 indicate reference values for the partitioning coefficient and the decomposition rates under no treatment effects, i.e. $\xi = 1$.

Using the obtained mean values of the posteriors with their respective ~~25-75~~5-95% uncertainty ranges, we calculated and plotted the response functions $f(X)$ with their intrinsic sensitivities $\partial f(X)/\partial X$, particularly for the treatment levels used in our experiment (Figure 4). The optimized functions ~~showed larger sensitivities~~ predict that decomposition rates increases as temperature, moisture and oxygen increases. For temperature, both the dependence and the sensitivity functions increase with temperature as well as the uncertainty in the predictions. For moisture, as the water filled pore space increases, decomposition rates also increase, but their intrinsic sensitive declines. Similarly, as oxygen levels increase, decomposition rates are predicted to increase but their sensitivity is expected to decline (Figure 4). The obtained functions also suggest larger sensitivities of decomposition rates with respect to temperature than with respect to moisture or oxygen. ~~At the upper part of the temperature range, decomposition rates were predicted to increase as well as the intrinsic temperaturesensitivity. Moisture and oxygen have both strong intrinsic sensitivities at the lower part of their ranges. Decomposition rates were highly sensitive at a narrow part of the oxygen range, while for moisture this range was wider (Figure 4).~~

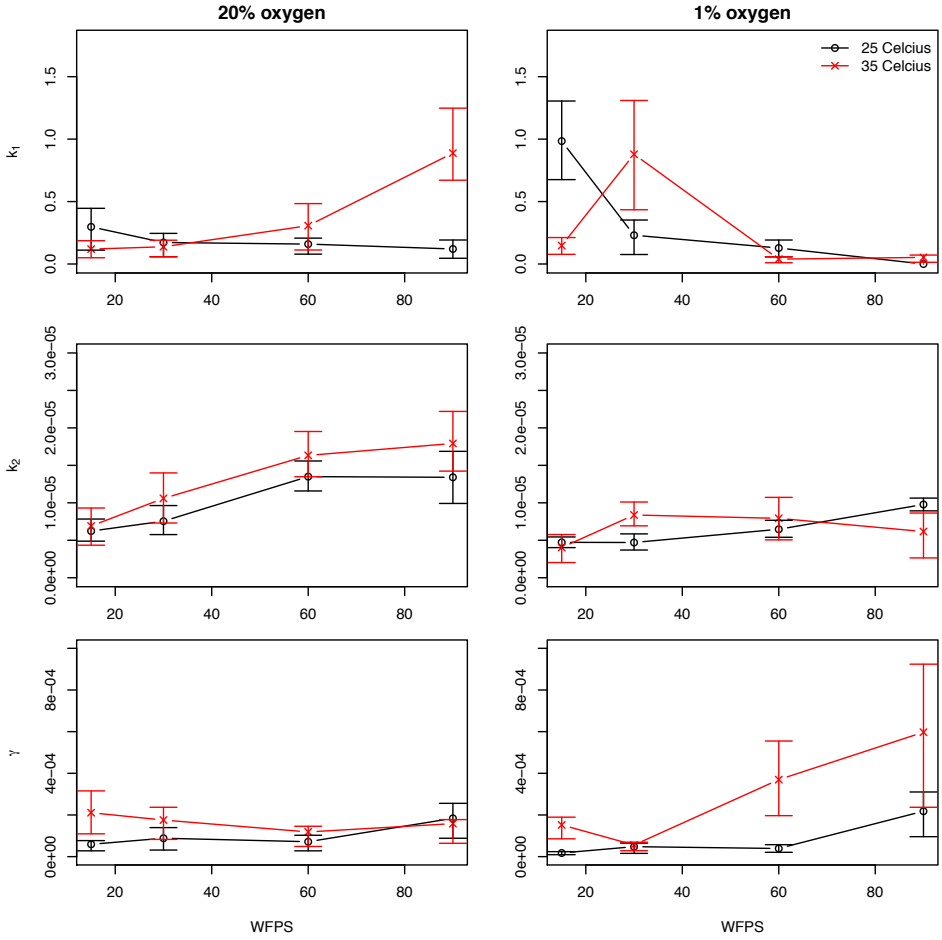

Figure 2. Results from the first model optimization procedure for the two pool model applied to each experimental treatment independently. Parameters optimized were k_1: decomposition rate of fast pool, k_2: decomposition rate of slow pool, γ: fraction of the total initial carbon in the fast pool. The experimental treatments were water-filled pore space WFPS (15, 30, 60, 90 %), oxygen concentration (1, 20%), and temperature (25, 35° Celcius). Arrows represent 25 and 75% quantiles of the distribution of the parameters obtained through Bayesian optimization.

Combining together the optimized functions into the term $\xi = f(T) \cdot f(M) \cdot f(O)$, we obtained the interacting effect of treatment level combinations on decomposition rates (Figure 5). Temperature, moisture and oxygen acted synergistically increasing decomposition rates in our experiment. Decomposition rates were twice as large at the highest treatment levels of temperature, moisture, and oxygen (35°C, 90%, 20%) than at the reference level ($\xi = 1$, k_1 and k_2 as in Table 1). For the lowest treatment levels (25°C, 15%, 1%), decomposition rates were reduced by a factor of 0.02 (two percent) from the reference level. Interactions between temperature and moisture in increasing decomposition rates were stronger when oxygen levels were high, but even at low oxygen levels increases in temperature and moisture resulted in small increases in decomposition rates.

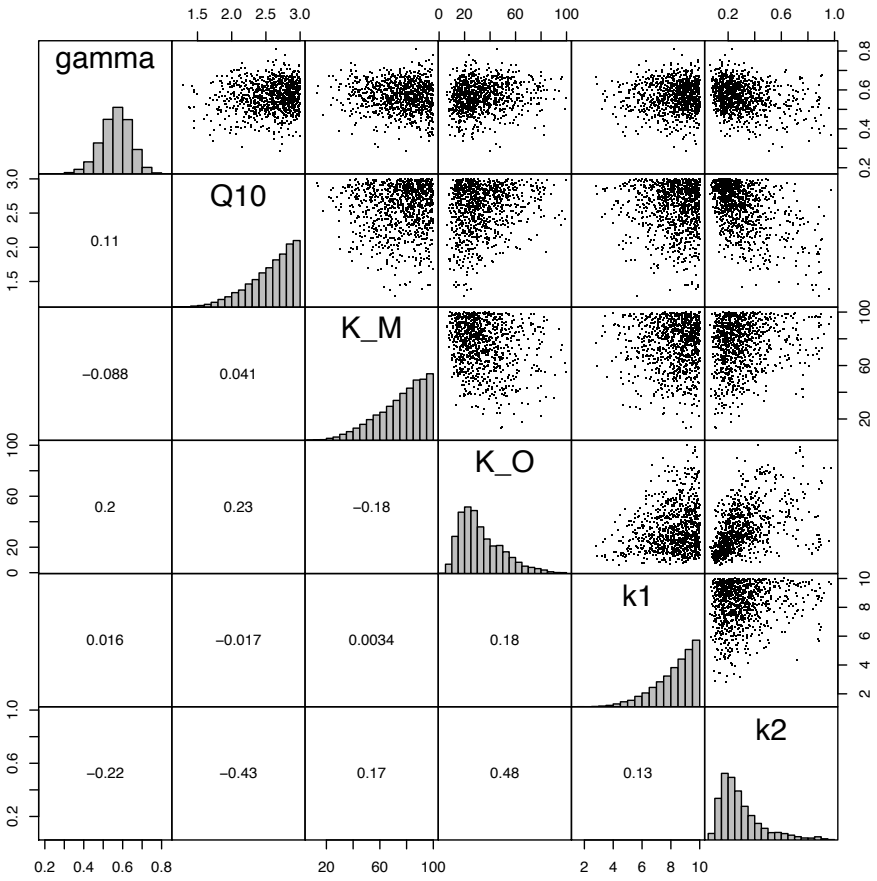

Figure 3. Posterior parameter values from the Bayesian optimization using the full model of equation (2). To avoid cluttering of the figure, only 1000 randomly samples values per posterior parameter set are plotted.

4 Discussion

The statistical comparison of the obtained respiration data as well as the results from these two modeling exercises demonstrated strong interactions among three main environmental factors that control decomposition. The factorial nature of our experiment allowed us to calculate intrinsic sensitivities for these three environmental factors. Moreover, without controlled conditions, the effects of one variable would have been confounded by others. For example, increases in temperature ~~almost always are~~ are often accompanied by decreases in soil moisture, and increases in moisture are generally accompanied by decreases in soil oxygen concentrations. Our experimental design, with a continuous flow of oxygen through the soil column, helped us to control oxygen concentrations independent on moisture, which avoided possible confounding effects.

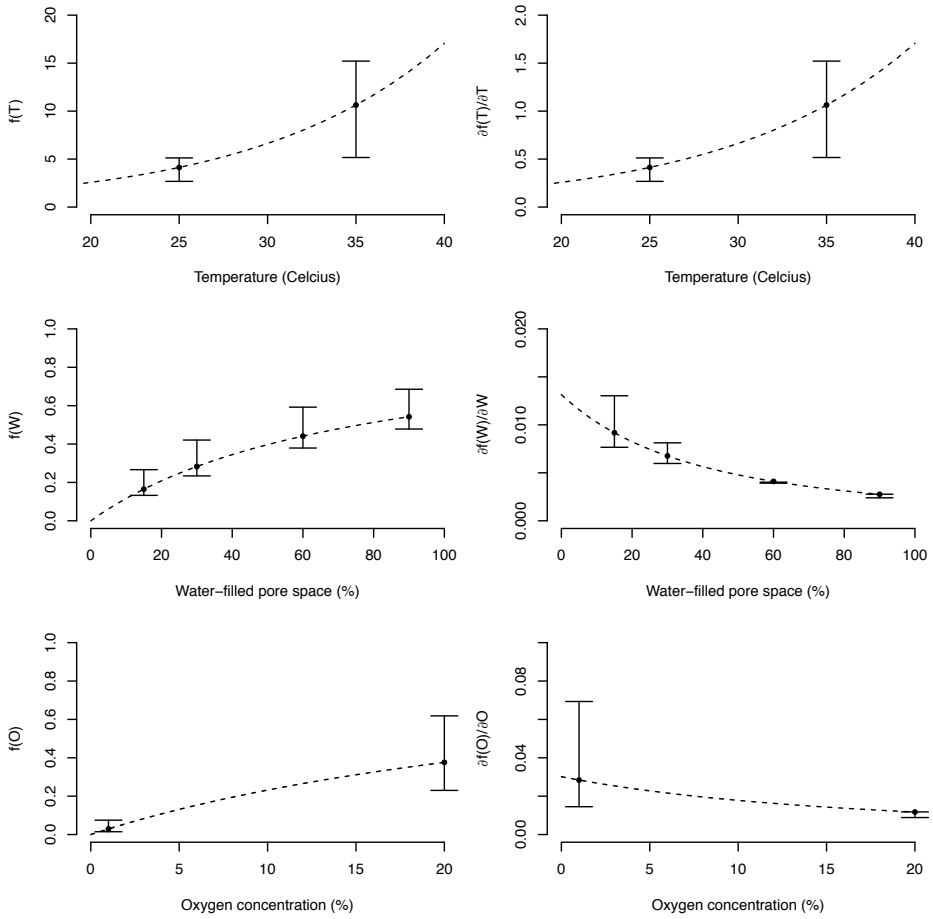

Figure 4. Shape of the response functions $f(T)$, $f(M)$, and $f(O)$ (dashed lines) calculated with the mean values of the posterior parameters, and their respective sensitivities $\partial f(T)/\partial T$, $\partial f(M)/\partial M$, and $\partial f(O)/\partial O$. Predictions for the treatment levels used in the experiment are presented as points with their respective 5-95% uncertainty.

Our results support previous work on the control of these three environmental variables on decomposition (Bunnell et al., 1977; Davidson et al., 2012, 2014). In particular, our results show that decomposition rates at the soil-core scale are strongly controlled by an interaction among three main environmental variables that generally change in concert with one another in the natural soil environment.

Tucker and Reed (2016) showed that the interaction between temperature and moisture play an important role for predicting soil respiration rates in dry soils. Similarly to our study, these authors did not find a decline in soil respiration rates at high temperatures. But rather, they found a strong interaction between an exponential function for temperature effects and a moisture function that reached a maximum at high moisture levels. This lack of decline of the moisture function is expected for dry soils that do not reach water saturation levels. The higher moisture range covered in our study shows more clearly that there is a

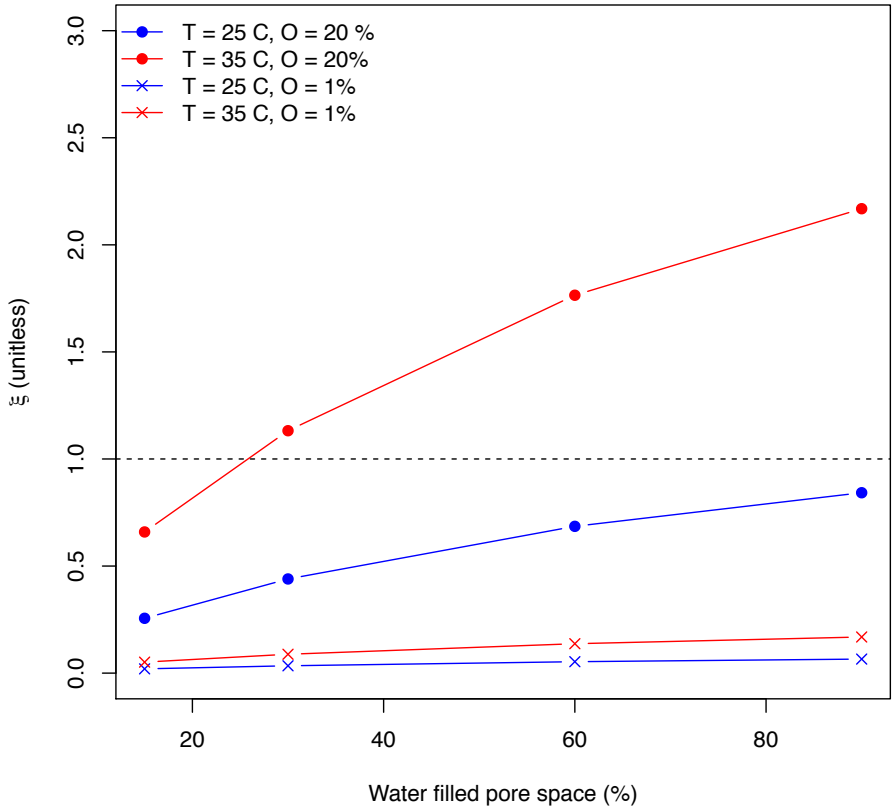

Figure 5. ~~Shape~~ Average value of the ~~response functions $f(T)$~~decomposition modifier $\xi = f(T) \cdot f(M) \cdot f(O)$, ~~$f(W)$, and $f(O)$ calculated with~~ predicted for the values of ~~the optimized parameters with their uncertainty~~temperature, moisture and ~~their respective sensitivities $\partial f(T)/\partial T$, $\partial f(W)/\partial W$,~~ oxygen levels applied to all treatment combinations in our experiment. Values above 1 increase decomposition rates and ~~$\partial f(O)/\partial O$~~values below 1 reduce them.

decline at high moisture levels and it is mostly driven by oxygen availability. One limitation of our study however, was the use of only two levels for the temperature and oxygen treatments, from which it is difficult to derive specific trends. This is a natural limitation of full factorial experiments, where the addition of extra treatment levels considerably increases logistical challenges.

Our modeling exercise, particularly the optimizations with the full dataset, helped us to better understand the combined effect of temperature, moisture, and oxygen in modifying decomposition rates for the soil we studied. The intrinsic sensitivity of decomposition with respect to temperature increased with temperature, but the intrinsic sensitivities with respect to moisture and oxygen decreased with increasing levels of these variables (Figure 4). Since there are complex interactions among these

three variables (Figure 5), specific responses due to their combined changes can only be predicted with the help of models. Although our model has a parsimonious representation motivated partly by the available data, additional details may be included for its use with field observations. For instance, the additional functions in the DAMM model used to represent pore space from bulk density and temperature controls on the K_X terms (Davidson et al., 2012) can help to capture additional complexity under field conditions that are not necessarily relevant under laboratory conditions. The DAMM model, or a variant of it, can be used to represent the term $\xi(t)$~~in a more complex model represented as a~~. Additionally, extra complexity due to higher heterogeneity of organic matter pools, stabilization and destabilization mechanisms, interactions among microbial enzymes and substrates, and vertical transport, can be incorporated into a larger set of differential equations (e.g. equation 1) dynamically modifying a set of state variables (Sierra and Müller, 2015).

5 Conclusions

Based on the experimental data for this ~~arctic~~ boreal soil and the model used, we conclude that decomposition rates can be high i) at high temperatures provided moisture and oxygen levels are not limiting, and ii) at high moisture levels provided oxygen concentrations are not limiting. We found no declines in decomposition rates at high temperatures as predicted by the MMRT~~. We interpret the mismatch of our results with the mentioned theoretical predictions as most likely due to differences in scale. We believe that at the scale of single enzyme-substrate pairs under controlled conditions (no changes in moisture levels) the predictions of the MMRT should still hold true (Hobbs et al., 2013; Schipper et al., 2014)~~; however, the lack of more temperature treatments in a wider temperature range may have been a limitation to find such theoretical optimum. Instead of a decline of respiration rates as promoted by increases in temperature alone, we found important interactions with soil moisture and oxygen concentrations that resulted in declines of respiration when these two variables were limiting. At the level of a soil core ~~or soil pit~~ with simultaneous changes in moisture levels, strong interactions among temperature, moisture and oxygen levels ~~override predictions~~ may override predictions on the temperature dependence at the scale of individual ~~enzymes~~enzymes-substrate pairs (Hobbs et al., 2013; Schipper et al., 2014) . These interactions exert a strong control on decomposition, and simultaneous changes of these variables under field conditions should determine the overall rate of decomposition in soils.

6 Code and data availability

Code and data necessary to reproduce all results from this manuscript are provided in the supplementary material. Furthermore, the soil incubation dataset used here is part of the soil incubation database (sidb) available as repository in GitHub (https://github.com/SoilBGC-Datashare/sidb).

Competing interests. The authors declare that they have no conflict of interest.

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